Staging ecology of black-tailed godwits in Portuguese rice fields and correlations with breeding season events

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Chapter 4

Population overlap and habitat segregation in wintering black-tailed godwits

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*Distinct breeding populations of migratory species may overlap both spatially and temporally, but differ in patterns of habitat use. This has important implications for population monitoring and conservation. We aim to quantify the extent to which two distinct breeding populations of a migratory shorebird, the black-tailed godwit (*Limosa limosa*), overlap spatially, temporally and in their use of different habitats during winter.*

We use mid-winter counts between 1990 and 2001 to identify the most important sites in Iberia for black-tailed godwits. Monthly surveys of estuarine mudflats and rice-fields at one major site, the Tejo estuary in Portugal in 2005-2007, together with detailed tracking of colour-ringed individuals, are used to explore patterns of habitat use and segregation of Icelandic godwits L. l. islandica *and the nominate continental subspecies* L. l. limosa.

In the period 1990-2001, over 66000 black-tailed godwits were counted on average in Iberia during mid-winter (January), of which 80% occurred at just four sites: Tejo and Sado lower basins in Portugal and Coto Doñana and Ebro delta in Spain. Icelandic black-tailed godwits are present throughout the winter and forage primarily in estuarine habitats. Continental black-tailed godwits are present from December to March and primarily use rice-fields.

Iberia supports c. 30% of the Icelandic population in winter and most of the continental population during spring passage. While the Icelandic population is currently increasing, the continental population is declining rapidly and, although the estuarine habitats used by Icelandic godwits are largely protected as Natura 2000 sites, the habitat segregation means that conservation actions for the decreasing numbers of continental godwits should focus on protection of rice-fields and re-establishment of freshwater wetlands.

Introduction

Distinct populations of migratory species can overlap in space and time during the non-breeding season, a period when energetic demands are high at temperate latitudes (Wiersma & Piersma, 1994) and there may be intense competition for food. Overlapping populations of a species may differ in their use of habitats (Telleria *et al*., 2001; Pérez-Tris & Telleria, 2002; Duijns *et al*., 2008), but this has rarely been documented (Baker & Baker, 1973). In part, this might reflect different populations being difficult to identify in the field (Pérez-Tris *et al*., 1999; Durell, 2000), particularly during the non-breeding season when ornamental traits are maintained at minimum levels. Habitat segregation in overlapping populations can have important conservation implications (Durell, 2000). Their description and analysis can potentially increase our understanding of key evolutionary and ecological processes, such as speciation and intra-specific competition (Newton, 2008).

In migratory waders (Charadrii), the majority of species are restricted to a few suitable habitats, which comprise only a very small area of each continent. Open habitats with low vegetation (e.g. wet grasslands and Arctic tundra) are typical breeding locations, while intertidal habitats and wetlands comprise the vast majority of the non-breeding habitats used by most species (van de Kam *et al*., 2004). At the species level, waders display a remarkable diversity of morphological traits, which have been suggested to facilitate resource partitioning in response to inter-specific competition (Zwarts & Wanink, 1984). This adaptive radiation of body size, leg length and particularly bill shape in relation to different foraging strategies allows quite fine-tuned specialisation to harvestable food types, and may reduce the need for spatial, temporal or habitat-based segregation among species in this community (Baker & Baker, 1973; Zwarts & Wanink, 1984). However, this foraging specialisation may simultaneously limit the use of other habitats and associated food resources (Weller, 1999), and thus constrain the capacity for within-species habitat or resource segregation. Within-species spatial segregation has been reported between age classes and sexes (Goss-Custard & Durell, 1983; Cresswell, 1994) and between distinct breeding populations (Burton *et al*., 2002). However, the extent to which populations concentrate their activity on different habitats is not often known (Baker & Baker, 1973; Newton, 2008). Without this information, protection and management of specific habitats may result in some populations being neglected. Identifying which populations might be constrained to particular habitats is therefore likely to be of importance in identifying conservation priorities for populations. This is particularly relevant for migratory waders as

many of the habitats on which they depend, such as estuarine flats and coastal wetlands, are currently heavily impacted by human activities both directly (e.g. through dredging, reclamation and over-harvesting of shellfish (Piersma *et al*., 2001; van Gils *et al*., 2006a)) and indirectly (e.g. through climate change impacts (Watkinson *et al*., 2004)).

Here we explore the non-breeding spatial and temporal overlap between two distinct breeding populations of black-tailed godwits (*Limosa limosa*). The continental population, *Limosa limosa limosa*, has its core breeding areas in The Netherlands and winters from Iberia to West Africa (Gill *et al*., 2002; Delany *et al*., 2009). The smaller population of Icelandic black-tailed godwits, *Limosa limosa islandica*, breeds almost entirely in Iceland and winters across western Europe, from Britain and Ireland in the north, to Iberia and Morocco in the south (Prater, 1975; Gill *et al*., 2002). Both *limosa* and *islandica* subspecies are present in Iberia during the non-breeding season (Stroud *et al*., 2004) and both overlap considerably in size and morphology (Prater *et al*., 1977). The recent population trends of these subspecies are highly divergent: the continental population is declining severely, while the Icelandic population is undergoing a sustained increase (Gunnarsson *et al*., 2005a; Gill *et al*., 2007). In Iberia, black-tailed godwits make extensive use of estuarine mudflats and rice-fields, and it has previously been suggested that there may be some habitat segregation between the subspecies (Moreira, 1994; Leitão, 1998). As the estuarine habitats are typically designated as Natura 2000 sites, while the rice-fields have no formal protection, habitat segregation could have important implications, particularly given the rapid decline of the continental godwit population for which loss and degradation of non-breeding habitat has been highlighted as a key issue (Gill *et al*., 2007).

We use mid-winter counts to determine the most important sites for black-tailed godwits in the Iberian overlap zone. We then use recent intensive survey information to describe the spatial and temporal overlap and the patterns of habitat use of the two subspecies. As the subspecies are almost impossible to identify accurately in winter plumage (Gunnarson *et al*., 2006a; Kuijper *et al*., 2006), we capitalise on the recent development of extensive colour-ringing programmes on the breeding grounds for each population, to assess their degree of habitat segregation throughout the winter. We conclude by recommending appropriate monitoring and conservation measures for the species in Iberia.

Methods

The most important sites for black-tailed godwits within the Iberian Peninsula were

identified based on census data compiled from national wetland surveys of Portugal and Spain, internal reports from governmental agencies, and published books and articles, covering the last three decades (e.g. CEMPA, 1982; Rufino & Neves, 1986; Rufino, 1993; Rufino & Costa, 1993; Costa & Rufino, 1994; 1996a; 1996b; 1997; Martí & del Moral, 2003). The majority of these counts originate from the pan-European waterbird survey scheme run by Wetlands International (Delany *et al*., 1999; Gilissen *et al*., 2001). Incomplete counts, either due to bad weather conditions or low spatial coverage, were excluded from analyses. January count data from Spain were only available between 1990 and 2001, thus the Iberia-wide analysis is restricted to this period.

Intensive field surveys of godwit use of different habitats took place in the winters of 2005-2006 and 2006-2007 at two major sites within Iberia: the Tejo (38° 57'N 8° 54'W) and Sado (38° 24'N 8° 48'W) lower basins in western Portugal. During the first winter (December 2005 to March 2006), the rice-fields of the Tejo lower basin were visited every fortnight and all black-tailed godwits counted. During the second winter (October 2006 to March 2007), both the rice-fields of Tejo and Sado and the estuarine areas of Tejo were searched systematically and black-tailed godwits were counted simultaneously at least once a month on both habitats. Nocturnal foraging of black-tailed godwits in this area is rarely recorded (Lourenço *et al*., 2008), and so surveys were carried out during daylight hours only. Black-tailed godwit flocks were regularly scanned for colour-ringed individuals before and after each count during the second winter. Only flocks containing one or more colour-ringed godwits from known breeding population were considered for this analysis (total number of sightings of individually marked godwits = 380, total number of separate observations of flocks = 170).

Colour-ringed black-tailed godwits of the *islandica* subspecies have been caught and ringed either on the Icelandic breeding grounds (Gunnarsson *et al*., 2005c; 2006b) or during post-nuptial migration on the Wash estuary (Gill *et al*., 2001a) on the east coast of England (total number of colour-ringed Icelandic godwits = 1639). Black-tailed godwits of the *limosa* subspecies used in this study were caught and ringed during the breeding season (Roodbergen *et al*., 2008; van den Brink *et al*., 2008; Schroeder *et al*., 2009a) in The Netherlands (total number of colour-ringed continental godwits = 384). Colour-ringing of these populations has taken place over several years, so the number of colour-ringed godwits estimated to be alive in the winter of 2006-07 was calculated from the annual totals (16-284 *islandica* colour-ringed each year between 1995 and 2006; 33 – 152 *limosa* colour-

ringed each year between 2002 and 2006) and published estimates of the survival rates for chicks during the first year of life (*islandica*: 50%; *limosa*: 54%) and annual survival rates for adults (*islandica*: 93%; *limosa*: 83%) (Gill *et al*., 2001a, 2007; Roodbergen *et al*., 2008). The ratio of marked birds from each population for the winter 2006-07 was then compared to the ratio of marked birds from each population in each habitat (mudflats and rice-fields) in that year, to assess the extent of habitat segregation between the populations and the proportion of godwits of each population using each habitat.

Results

Key sites for black-tailed godwits in Iberia

Table 4.1: January counts of black-tailed godwits on major sites in Portugal and Spain between 1990 and 2001. All sites with two counts > 500 individuals in any year are included, and also Umia-O Grove which has fewer birds but is regularly used. Site codes are given for spatial reference of each site on Fig. 4.1.

Site	Min.	Max.	Average	National(%)	Cumulative(%)	Code
Portugal						
Tejo estuary & rice-fields	1020	48980	23929	75.10	75.10	1
Sado estuary & rice-fields	241	20030	4331	13.59	88.69	2
Ria Formosa	551	4474	2455	7.71	96.41	3
Ria de Aveiro delta	356	5022	485	1.52	97.93	4
Castro Marim saltpans	174	1570	528	1.66	99.59	5
Spain						
Coto Doñana	5000	55190	24638	71.55	71.55	6
Ebro delta	0	4797	3474	10.09	81.63	7
Palazuelos rice fields	0	9026	2257	6.55	88.19	8
Cadiz Bay	0	4250	1139	3.31	91.49	9
Odiel marshes	102	722	381	1.11	92.60	10
Santa Pola saltpans	0	756	343	1.00	93.60	11
Complex Umia-O Grove	23	491	237	0.69	94.28	12

Between 1990 and 2001, Portugal supported an average of 30000 black-tailed godwits in January, with almost all occurring within just five distinct wetland sites (Table 4.1). The Tejo and Sado river basins alone held c. 88% of the total number of godwits recorded in Portugal between 1990 and 2001.

In Spain the situation is similar, with an average of 34000 godwits recorded in January between 1990 and 2001, and two sites, Coto Doñana and Ebro Delta, holding c. 81% of the godwits, although many more sites were used by the species over the census period. In some sites, such as Palazuelos rice-fields in Extremadura province and Odiel Marshes in Andaluzia province, godwits were only recorded during the initial years of the census period, as no published counts have taken place there since 1995. However, during recent years J.A. Masero and co-workers have recorded numbers averaging about 24000 individuals during mid or late February on the recently developed rice-fields of Extremadura, making this a site of major importance for godwits in Iberia (Kuijper *et al*., 2006; Sánchez-Guzmán *et al*., 2007). Other sites, such as Santoña marshes, have had increasing numbers since 1994 (to a maximum of 300 in 2000) which are reported to have continued increasing since then (Navedo *et al*., 2007).

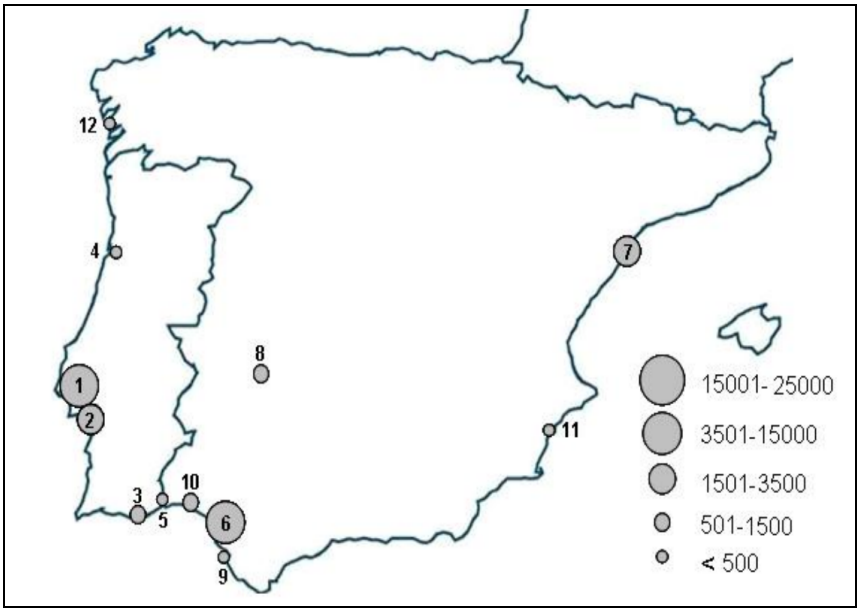

Figure 4.1: Location of important sites for black-tailed godwits in the Iberian Peninsula. Numbers refer to average January counts for the period 1990-2001. The eleven marked sites supported c. 95% of the total number of godwits in the region during this period.

In the Iberian Peninsula, the four most important sites for the black-tailed godwits (Tejo and Sado lower basins both on the west coast of Portugal, Coto Doñana in southern Spain and Ebro delta in eastern Spain, Fig. 4.1), all have large areas of two distinct habitats that are used by the species: rice-fields and estuarine mudflats (Martí & del Moral, 2003).

Seasonal and geographic overlap of continental and Icelandic godwits

During the northward migration from west Africa, continental godwits make an extended stop-over in Iberia from late December to early March (Lourenço *et al*., in press a; Chapter 6). During this period, several thousand black-tailed godwits join the wintering flocks at the major Iberian sites using both the mudflats and the rice-fields. Consequently, at the start of January, there are typically fewer than 10000 godwits present on the Tejo and Sado lower basins, but numbers increase rapidly during January to over 50000 individuals (Fig. 4.2).

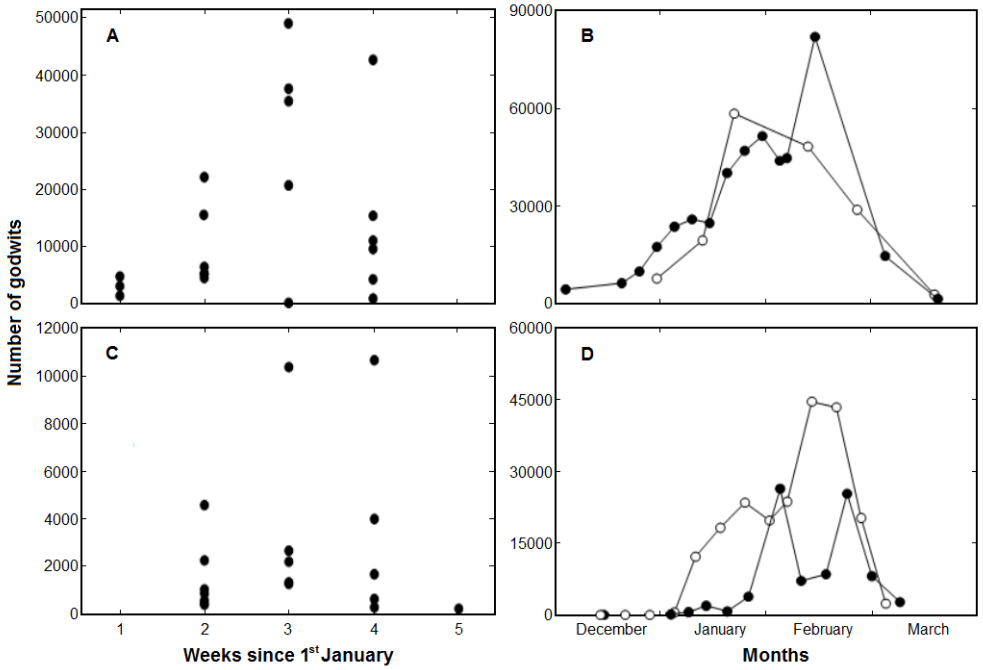

Figure 4.2: Variation in numbers of black-tailed godwits recorded in each of the first five weeks of the year between 1978 and 2006 at Tejo (A) and Sado (C), and at the Tejo lower basin during two consecutive winters 15 years apart: (B) 1991-1992 (filled circles) and 1992-1993 (open circles); (D) 2005-2006 (filled circles) and 2006-2007 (open circles).

January counts vary greatly among years on the Tejo estuary (mean = 23929, SD = 16571, n = 11), Coto Doñana (mean = 24638, SD = 16008, n = 11) and Sado estuary (mean = 4341, SD = 5954, n = 11). On the Tejo estuary, the variance in counts is significantly lower during the first half of the month than during the second half (Brown-Forsythe Levene's test: W = 7.12, p = 0.016, n = 20, Fig. 4.2). The same does not apply to the counts in the Sado (W = 1.24, p = 0.28, n = 18), probably due to the lack of any counts in the first week of January, but the high variance in counts in late January is also apparent at this site (Fig. 4.2).

The variation in counts at the Tejo and Sado lower basins (Fig. 4.2) is clearly a consequence of the timing of passage of the continental subspecies. Around 15000 *islandica* godwits (for which the total population size is c. 50000) are believed to winter in the whole of Iberia (Gunnarsson *et al.* 2005b). Thus the January counts in Iberia comprise a large proportion of continental godwits.

Habitat segregation of continental and Icelandic godwits

A total of 231 sightings of individually marked Icelandic and 149 sightings of individually marked continental black-tailed godwits were recorded on the mudflats and rice-fields of Tejo and Sado during the winter of 2006-07. The distribution of these godwits across habitats in each month varied greatly, with 1.7 to 5.5 times more colour-ringed Icelandic godwits than continental godwits using the estuarine mudflats (Fig. 4.3). By contrast, on the rice-fields, the number of colour-ringed continental godwits was 1.4 to 2.5 times higher than the number of Icelandic godwits (Fig. 4.3). The overall pattern of habitat segregation of the two populations is significantly different from an even distribution across the habitats, ($\chi^2_3 = 281.16$, $p < 0.01$), and only three of the 37 colour-ringed individuals that were recorded on more than one occasion were seen in both habitats.

Simultaneous counts of black-tailed godwits at the Tejo rice-fields and estuary depict the different patterns of use of these habitats (Fig. 4.4). While c. 3000 godwits are present on the mudflats throughout the winter period, counts on the rice-fields indicate that over 20000 black-tailed godwits are present during a relatively short period in January and February. The influx of continental godwits into the Tejo lower basin during January and February therefore appears to have little effect on the number of godwits present on the estuarine mudflats.

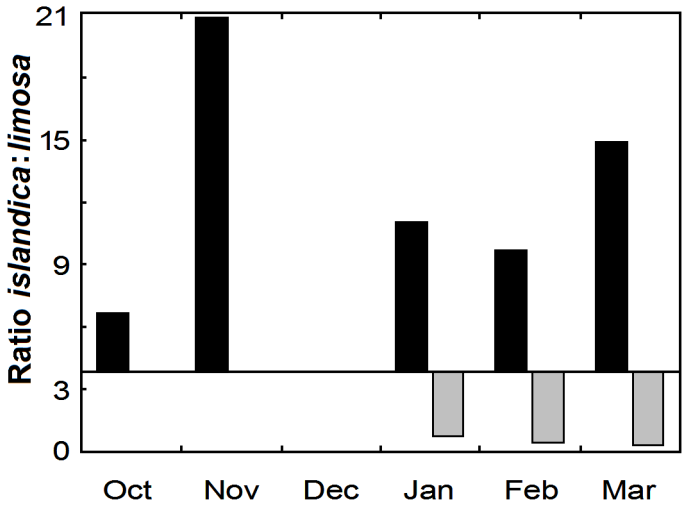

Figure 4.3: Monthly variation in the ratio of *islandica*:*limosa* colour-ringed black-tailed godwits on the estuarine mudflats (black) and the rice-fields (grey) of Tejo and Sado during 2006-2007. The horizontal line indicates the population-wide ratio of colour-ringed *islandica*:*limosa* estimated for the winter of 2006-2007 (ratio = 3.8). No colour-ringed continental godwits were recorded on the estuary during December, and no colour-ringed godwits were recorded on the rice-fields prior to January.

The monthly ratio of colour-ringed individuals from each population using each habitat during the winter was used to estimate the proportion of godwits from each population present on each habitat on a given month. On average, 76% of godwits on the estuarine mudflats are of the Icelandic population whereas 90% of godwits on the rice-fields are of the continental population. These proportions vary seasonally (Fig. 4.4), reflecting the phenology of both populations and the absence of rice-field usage prior to January. In October, the c. 3000 godwits on the estuary are estimated to comprise roughly equal proportions of both populations (Fig. 4.4) as some Icelandic godwits have not yet arrived and some continental godwits stop off on their way to west Africa. At this time of year the rice-fields areas are unharvested and too dry for godwits (Lourenço & Piersma, 2008a; Chapter 3). From November to January, only around 500-1000 continental godwits are estimated to occur on the estuary, together with an estimated 2000-3000 Icelandic godwits (Fig. 4.4). By contrast, the rice-fields are estimated to support more than 20000 continental

godwits in January but a maximum of only c. 1000 Icelandic godwits (Fig. 4.4).

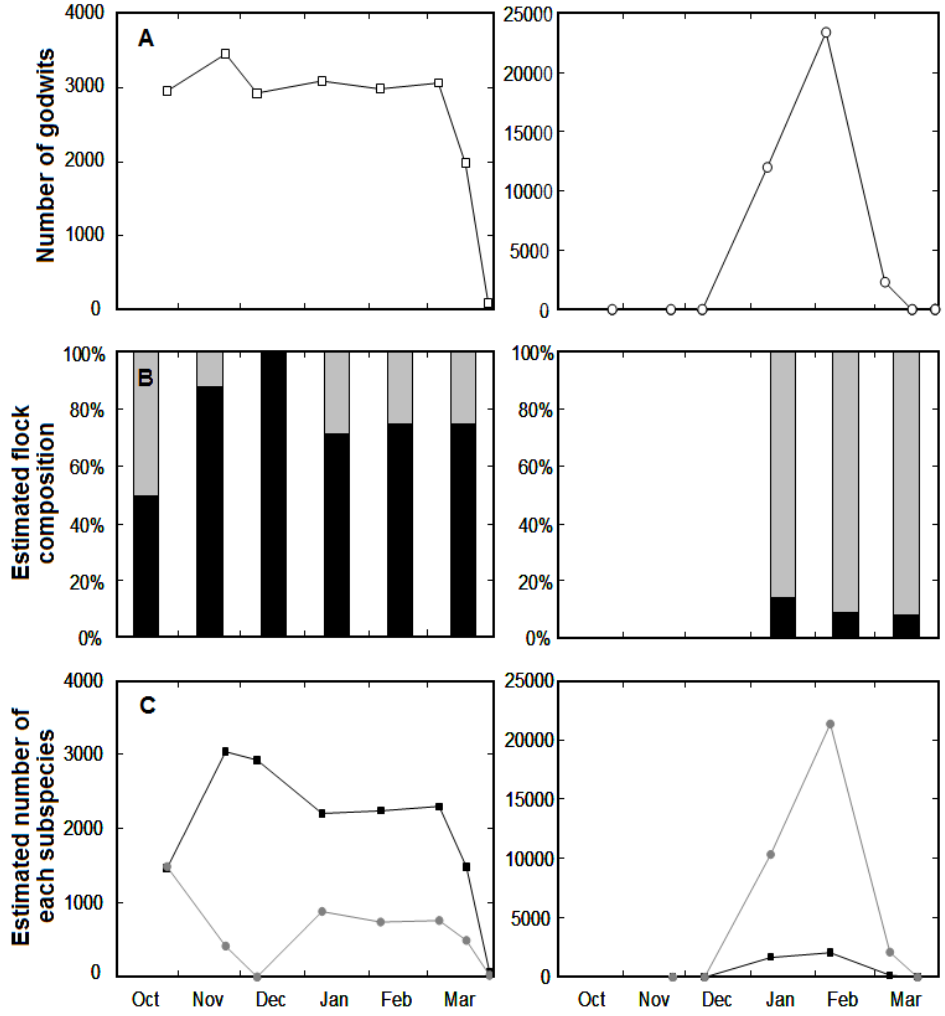

Figure 4.4: Monthly variation on estuarine (left column) and rice-field (right column) habitats of (A) total numbers of black-tailed godwits on the Tejo lower basin during 2006-2007, (B) the proportion of colour-ringed Icelandic (black) and continental (grey) black-tailed godwits and (C) the estimated numbers of each subspecies present on each habitat throughout the winter.

Discussion

Between 1990 and 2001, both Icelandic and continental black-tailed godwits in the Iberian Peninsula congregated on four major sites during the non-breeding season. Mid-winter counts show that the lower basins of Tejo and Sado in Portugal, together with Coto

Doñana and Ebro delta in Spain, held more than 80% of the black-tailed godwits recorded in Iberia between 1990 and 2001. All four sites contain a mosaic of estuarine mudflats and rice-fields with individuals from both populations being present on both habitats. However, in the Tejo there is clear habitat segregation, with Icelandic godwits primarily occurring on mudflats and continental birds primarily using rice-fields. This pattern of habitat segregation might occur throughout the main Iberian sites.

Individuals from both black-tailed godwit populations are present in Iberia from October until March, but the overlap is most apparent when the massive flocks of continental godwits (c. 15000 to 45000) arrive in the peninsula from late December, when the rice-fields become available (Lourenço & Piersma, 2008a; Chapter 3), to early March and join the overwintering flocks (c. 150 to 3000). It is noteworthy that comparison of peak counts in the Tejo lower basin during the early 1990s and 2005-07 indicates an approximately 50% decline in numbers of godwits in this area (Fig. 4.3). This reduction is consistent with the major declines in numbers of continental godwits in recent years (Gill *et al*., 2007). Although counts made during the 1990s were carried out at dawn when godwits leave the estuarine roost towards the rice-fields and the later counts were made by visiting all the rice-fields during day time, this is unlikely to contribute significantly to the different numbers in the two time periods as all suitable rice-fields were surveyed during the more recent counts.

In more recent years, godwits have occurred in increasing numbers in the inland rice-fields of Extremadura, western Spain (Sánchez-Guzmán *et al*., 2007). Our estimate of the proportion of Icelandic godwits on the rice-fields (c. 10%) is very similar to estimates from Extremadura (Masero *et al*., 2009), despite those inland rice-fields having no estuarine habitats in close proximity. Icelandic godwits therefore do not appear to be common on rice-fields, even when no other habitat is available.

Although godwits of both subspecies occur on mudflats and rice-fields, there is a clear tendency for Icelandic godwits to use the estuarine mudflats and continental godwits to use the rice-fields as foraging locations (Moreira, 1994; Lourenço & Piersma, 2008a; Chapter 3). Given the morphological similarity of both subspecies, and the fact that some individuals move between the habitats, the reasons for this habitat segregation are not immediately obvious. Estuarine mudflats and rice-fields may provide structurally similar foraging conditions, as both comprise the soft, moist sediments that black-tailed godwits can probe to extract food items. However, whereas black-tailed godwits on estuarine

mudflats are ingesting animal prey (Moreira, 1994; Gill *et al*., 2001b), godwits on the rice-fields forage almost exclusively on plant material, primarily rice seeds (Lourenço & Piersma, 2008a; Chapter 3). It is therefore possible that there is a physiological basis to the habitat segregation and that switching between habitats may incur several costs: (1) changing between animal and plant diets is likely to require modifications of the gastrointestinal tract to process such different food types (Piersma *et al*., 1993; Dekinga *et al*., 2001), and to assimilate different nutrients efficiently (e.g. protein versus carbohydrates and fibre) (Starck, 1999; Castro *et al*., 2008; Santiago-Quesada *et al*., 2009); (2) habitats with a higher saline load may require a larger salt gland (Staaland, 1967; Rubega & Oring, 2004), in order to excrete a more concentrated secretion, and thus tolerate higher salt loads (Staaland, 1967); (3) estuarine and freshwater habitats may differ in the prevalence of pathogens and parasites (Piersma, 1997; Mendes *et al*., 2005) or levels of toxic chemicals (Tavares *et al*., 2007), which may also require physiological adaptations and have longer-term implications for activation of the immune response or the bioaccumulation of toxic substances (Scheuhammer, 1991; Hanssen *et al*., 2004).

Continental godwits use mostly freshwater habitats in the African winter grounds, particularly the rice-fields of Senegal and Guinea Bissau (Tréca, 1994; Gill *et al*., 2007; Zwarts *et al*., 2009). The costs associated with switching to a saline habitat, alongside an energetically demanding migratory flight between west Africa and Europe, may explain why continental godwits avoid estuarine mudflats in late winter. On departure from Iberia, both subspecies migrate to The Netherlands (and to a lesser extent eastern England) where the continental godwits breed and the Icelandic godwits refuel before migrating to Iceland (Gill *et al*., 2007).

Conservation implications of habitat segregation in distinct godwit populations

The clear differences in habitat use and phenology of the two populations of black-tailed godwits in Iberia can inform targeted conservation and monitoring efforts. Firstly, although January is considered to be the month when migratory movements of waterbirds are less common (Martí & del Moral 2003; Stroud *et al*., 2004; Delany, 2005), this is not the case in southwest Europe for this species. The extensive movement of continental godwits from Africa to Iberia during January and February results in huge variability in the mid-winter (January) counts. Effective monitoring of both godwit populations in Iberia therefore requires counting periods to be scheduled in accordance with the relevant

migration patterns, as counts in December or early January will largely comprise Icelandic godwits whereas counts in late January and February will also capture continental godwits. Secondly, the lack of any legal protection on more than 80% of the rice-field area in the lower basins of the Tejo and Sado rivers is of great concern given the huge proportion of the rapidly declining continental godwit population that depends on this habitat. Widespread drainage of wetlands has left rice-fields as virtually the only remaining freshwater habitat for foraging waders, and rice-fields are now of great importance for many species (Elphick 2000; Lourenço & Piersma, 2009; Chapter 2). Protection of key wetland sites (including rice-fields) in southern Europe and Africa is of critical importance in maintaining threatened populations that depend upon these habitats (Gill *et al*., 2007; Lourenço & Piersma, 2009; Chapter 2).

Habitat segregation of overlapping breeding populations during winter might be more common than is currently known, and might have important implications for the conservation of other migratory species. Detailed studies on habitat use of overlapping populations are scarce but can inform the development of conservation policies. The present widespread decline of many wader species might also be influenced by threats to small patches of habitat with paramount importance for some species. This can be particularly acute for populations where conservation and habitat management actions already employed in some areas of the range have failed to reverse population declines, as is the case for breeding continental black-tailed godwits (Kleijn *et al*., 2001). Without detailed studies on overlapping populations we are unaware of such events and thus unable to effectively protect these populations.

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